

COMPARATIVE ANATOMY OF THE LEAF-BEARING  
CACTACEAE, VIII<sup>1</sup>THE XYLEM OF PERESKIAS FROM SOUTHERN  
MEXICO AND CENTRAL AMERICAI. W. BAILEY<sup>1</sup>

AS DEMONSTRATED IN the second paper of this series (Bailey, 1961a), there are three distinct categories of pereskias that can be differentiated by consistent differences in the form and distribution of sclereids in their secondary phloem. *Pereskia konzattii* Britt. & Rose of southern Mexico, *P. autumnalis* (Eichlam) Rose of Guatemala and *P. nicoyana* Web. of Costa Rica belong in one category which includes *P. aculeata* Mill. and such pereskias of Peru and Bolivia as *P. humboldtii* Britt. & Rose, *P. vargasii* H. Johnson, *P. weberiana* K. Schum. and *P. diaz-romeroana* Cárđ. It is of interest, both morphologically and taxonomically, to determine whether there is cogent evidence in the various organs and parts of these plants, other than in their syncarpous ovaries, which justifies separating them in independent genera, viz. *Pereskia* and *Rhodocactus* (Berg.) Knuth. In this paper evidence from the xylem will be described and discussed.

The pereskias of southern Mexico, Guatemala and Costa Rica are trees which attain heights of eight to ten meters at maturity. They are characterized by forming relatively massive trunks which at times attain diameters of as much as forty centimeters. My collections of *Pereskia konzattii*<sup>2</sup> are numerous, stems of varying sizes having been kindly collected and preserved for anatomical investigation by Norman Boke (5 collections), Duncan Clement, R. L. Dressler, King and Diboll, H. E. Moore, Jr. (two collections) and Sharp and Hernández. For comparison I have two collections of *P. autumnalis* made by Dr. Moore and one of *P. nicoyana* sent to me by Dr. Rodríguez. The xylem of the secondary body in stems and roots of the three pereskias is similar, exhibiting comparable ranges of structural variability in different parts of a mature tree.

The most characteristic and significant trend of diverging anatomical specialization occurs in the basal parts of the trunks of *Pereskia konzattii*,

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<sup>2</sup> This species may prove to be the same as *Pereskia pititache* Karwinsky. Britton and Rose (1919) in reducing Karwinsky's species to synonymy with *Pereskopsis pititache* evidently based their description upon a plant sent to the New York Botanical Garden by M. Simon of Paris. This particular clone appears to have differed from Karwinsky's plant in being a representative of *Pereskopsis* rather than of *Pereskia*.

*P. autumnalis* and *P. nicoyana*. In preceding papers of this series I noted that in the larger young stems of *P. sacharosa* Griseb. and *P. aculeata* (Bailey, 1962), and likewise in those of Andean pereskias (Bailey, 1963), there is a tendency toward increase in the circumference of the primary vascular cylinder and in the diameter of the pith subsequent to the initiation of cambial activity in the fascicular parts of the eustele. In stems of these species broadening of the parenchymatous gaps in the eustele may or may not involve concomitant broadening of the inner parts of the first-formed, lignified, multiseriate rays of the secondary body. In dissecting the main stem and branches of *P. conzattii*, one finds that the basal part of the trunk has a much enlarged pith (up to five centimeters or more in diameter at times) having what appears superficially to be stellate projections which extend outward for varying distances into the xylem of the secondary body. Similar structures occur in the trunks of *P. autumnalis* and *P. nicoyana*. That such projections of soft tissue are not parts of the primary body is shown in FIGS. 1, 2, 4, 11, and 14.

When cambial activity is initiated in the broadening interfascicular parts of the eustele, its derivatives have thin, unligified walls and retain a capacity for division and enlargement (note the transverse expansion of ray cells in FIG. 11). This broadening of multiseriate rays, concomitant with lateral expansion of the parenchymatous gaps in the eustele, facilitates continued increase in the diameter of the pith for more or less extended periods of time. In fully matured stems, the expanded rays may contain patches of lignified ray cells (FIGS. 1, 4, and 14). Although their outward extensions are lignified, the rays tend at least for a time to be conspicuously broader than the multiseriate rays of secondary xylem that is subtended by fascicular parts of the eustele (FIGS. 1, 2, 11, and 14). It should be noted in this connection that, as in stems and roots of *Pereskia aculeata* and in roots of the Andean pereskias, the thin-walled unligified parenchyma of the secondary xylem contains characteristic druses of calcium oxalate (FIGS. 1, 2, and 4), resembling those that occur so commonly in unligified tissue of the pith, phloem and cortex of the leaf-bearing Cactaceae (Bailey, 1961b).

The first-formed secondary xylem in branches and smaller stems from the upper part of mature trees of *Pereskia conzattii*, *P. autumnalis* and *P. nicoyana* tends to be of more nearly normal dicotyledonous structure. For example, in FIG. 3, the multiseriate rays which extend radially outward from parenchymatous gaps of the eustele are lignified throughout and are only slightly broader than those in wedges of secondary xylem subtended by fascicular parts of the primary body. There obviously has been some lateral expansion of the interfascicular parts of the eustele during earlier ontogenetic stages of development, but the tangentially enlarged parenchymatous cells of these parts have become lignified. By comparing sections from upper parts of a mature tree with others from successively lower levels various stages in the ontogenetic and phylogenetic modification of first-formed multiseriate rays may be reconstructed.

Turning to the structure of fully lignified parts of the secondary xylem,

one finds similarities to that of *Pereskia sacharosa* in stems of comparable diameter from equivalent parts of a tree. The vessels occur singly and in small clusters and are diffusely distributed (FIG. 3), or may at times exhibit more or less conspicuous zonation (FIG. 5). The wood parenchyma is scanty paratracheal (FIG. 9). The libriform fibers are slender, thick-walled and function in the storage of starch. The lignified multiseriate rays, except in the first-formed secondary xylem of the trunk, are not excessively broad and exhibit ranges of variability in form and internal structure comparable to those which occur in *P. sacharosa*. The first-formed multiseriate rays in wedges of secondary xylem subtended by fascicular parts of the eustele are comparatively narrow (FIGS. 1, 2, and 3), and are vertically extensive (FIGS. 11, 14, and 15). As in *P. sacharosa* and many other dicotyledonous trees (Bailey, 1962), the multiseriate rays become dissected sooner or later into lower rays during their radial extension outward (FIG. 13). Such derivative parts tend to become somewhat broader and tangentially displaced during increase in circumference of the cambium (FIGS. 13 and 16). The cells of the rays vary conspicuously in size, form and orientation even in comparable parts of the stems of a single plant. The first-formed parts of the multiseriate rays, at least in small branches from the upper part of a tree, tend to be composed of somewhat vertically elongated cells, i.e. of "erect" orientation. The subsequently formed outward extensions of the rays, as in *P. sacharosa*, commonly are composed of more or less isodiametric cells or of varying mixtures of isodiametric and radially elongated or "procumbent" ones. In some cases (FIGS. 13 and 15), erect cells may occur along the sides of the multiseriate rays, as in *P. sacharosa*.

The most conspicuous differences in the lignified secondary xylem of such pereskias as *Pereskia conzattii* and *P. autumnalis*, in comparison with that of *P. sacharosa*, occur in the outer tissue of large trunks of the former species which greatly exceed the largest stems of *P. sacharosa* in diameter. In this tissue the vessels are jacketed by abundant wood parenchyma (FIGS. 10 and 12). Furthermore, the vessels and parenchyma occur in concentric patterns alternating with dense zones composed largely of libriform fibers (FIGS. 6 and 12). In addition, the multiseriate rays tend to be composed internally of conspicuously procumbent cells (FIGS. 10 and 12). Although the vessels frequently are larger (200 millimeters or more in diameter) than in earlier formed secondary xylem (compare FIGS. 9 and 10), this is not invariably the case. In some smaller stems there may be precocious enlargement of vessels to equivalent size (compare outer part of FIG. 5 with FIG. 6). Nor are the multiseriate rays invariably wider than in the xylem of all smaller stems (compare FIGS. 5 and 6, 13 and 16). The width and the abundance of multiseriate rays in the secondary xylem is highly variable as in stems of *P. sacharosa*.

My collections of roots of *Pereskia conzattii* and of allied taxa from Guatemala and Costa Rica are limited in number, but in those that I have, the secondary xylem is of normal dicotyledonous structure, resembling that which occurs in roots of *P. sacharosa*. In none of them are there

indications of multiseriate rays composed of unligified cells or of the occurrence of patches or zones of unligified parenchyma. The rays which may broaden more precociously than in stems are ligified throughout their radial extension. The vessels, which frequently tend to be more numerous and larger than in equivalent tissue of stems, occur singly and in small crowded clusters (FIG. 7). The wood parenchyma is scanty paratracheal, but may at times exhibit a tendency to become more abundant in the outermost xylem of very large old roots.

#### DISCUSSION

*Pereskia konzattii*, *P. autumnalis* and *P. nicoyana* occur in a category of leaf-bearing cacti that exhibit consistent similarities in the form and distribution of sclereids in their secondary phloem (Bailey, 1961a). *Pereskia aculeata* and the Andean pereskias likewise occur in this distinct anatomical category. On the contrary, *P. sacharosa* falls into a second category with *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak and *P. tampicana* Web., whereas *P. colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose and *P. portulacifolia* Haw. belong in a third distinct category.

In *Pereskia aculeata*, in contrast to *P. sacharosa* (Bailey, 1962), the secondary xylem exhibits conspicuous trends of anatomical modification in both stems and roots. Therefore, this species cannot be considered to be one of the most, if not the most, primitive living representatives of the Cactaceae, except possibly in the supposedly "superior" position of its syncarpous ovary. Similarly, the excessive structural modifications of the roots of the Andean pereskias (Bailey, 1963) negates the conclusion that these species have retained comparatively primitive morphological features throughout both their reproductive and vegetative organs.

In the case of the pereskias from southern Mexico and Central America, although the secondary xylem in general tends to resemble that of *Pereskia sacharosa*, there obviously are excessive modifications of part of the first-formed multiseriate rays in the basal parts of the trunks of these trees. Similar trends of excessive divergent phylogenetic specialization do *not* occur in other pereskias that have been included in the putative genus, *Rhodocactus*, as will be demonstrated in the next two papers of this series, but do occur in *Pereskiopsis aquosa* (Web.) Britt. & Rose and possibly in other species of *Pereskiopsis* and *Quiabentia* as will be shown subsequently. Thus, there is no cogent complementary anatomical evidence which justified placing *P. konzattii*, *P. autumnalis*, and *P. nicoyana* in *Rhodocactus* as at present constituted. It should be noted in this connection that in preliminary investigations of immature and mature flowers of these three species Professor Boke and I find no conclusive evidence that the ovaries are much more deeply depressed in the tissue of the torus than, for example, in the case of *P. aculeata*. Rather, we have found that the flowers of the supposedly most primitive cacti need to be reinvestigated in detail by modern methods of clearing and serial sectioning.

In the case of the Cactaceae as a whole there obviously are many trends of parallel evolution. Relatively close similarities are not always indicative of close genetic relationship. Conversely, morphological differences in one organ or part, which frequently are quantitative rather than qualitative, may not necessarily be indicative of remote relationship when evidence from other organs or parts is taken into consideration. A more rational division of the family into subfamilies, tribes, genera and species may possibly be attained only by synthesizing and harmonizing evidence from all organs and parts of the plants.

Anatomical evidence presented thus far indicates that *Pereskia sacharosa* has retained a normal type of secondary xylem which may possibly have characterized ancestral Cactaceae. This structural form of xylem is retained in certain parts of the stems of *P. aculeata*, but has been drastically modified in other parts of its stems and in its roots. It tends to persist in stems of the Andean pereskias, but has been highly modified in the roots of these plants. It has tended to persist in the roots and most parts of the stems of pereskias from southern Mexico, Guatemala and Costa Rica, but has been extensively modified in the basal parts of their trunks. At present, such anatomical evidence by itself and without strong corroborative support from other parts of the plants is of uncertain reliability in determining genetic relationships.

#### LITERATURE CITED

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#### EXPLANATION OF PLATES

##### PLATE I

FIGS. 1-4. Transverse sections of stems showing incipient stages in the formation of multiseriate rays. 1, *Pereskia conzattii* [Dressler] stem 10 cm. in diameter, pith 2 cm. diameter,  $\times 11$ . 2, *P. conzattii* [Sharp & Hernández] stem 7 cm. in diameter, pith 3 cm. in diameter,  $\times 11$ . 3, *P. autumnalis* [Moore 8210] stem 7 cm. in diameter, pith 3.5 cm. in diameter,  $\times 11$ . 4, *P. nicoyana* [Rodríguez 662] stem 7.5 cm. in diameter, pith 2 cm. in diameter,  $\times 22$ .

## PLATE II

FIGS. 5-8. Transverse sections of secondary xylem. 5, *P. conzattii* [Sharp & Hernández] stem 7 cm. in diameter,  $\times 11$ . 6, *P. autumnalis* [Moore 8210] stem 18 cm. in diameter,  $\times 11$ . 7, *P. conzattii* [Sharp & Hernández], old root,  $\times 11$ . 8, *The same*,  $\times 34$ .

## PLATE III

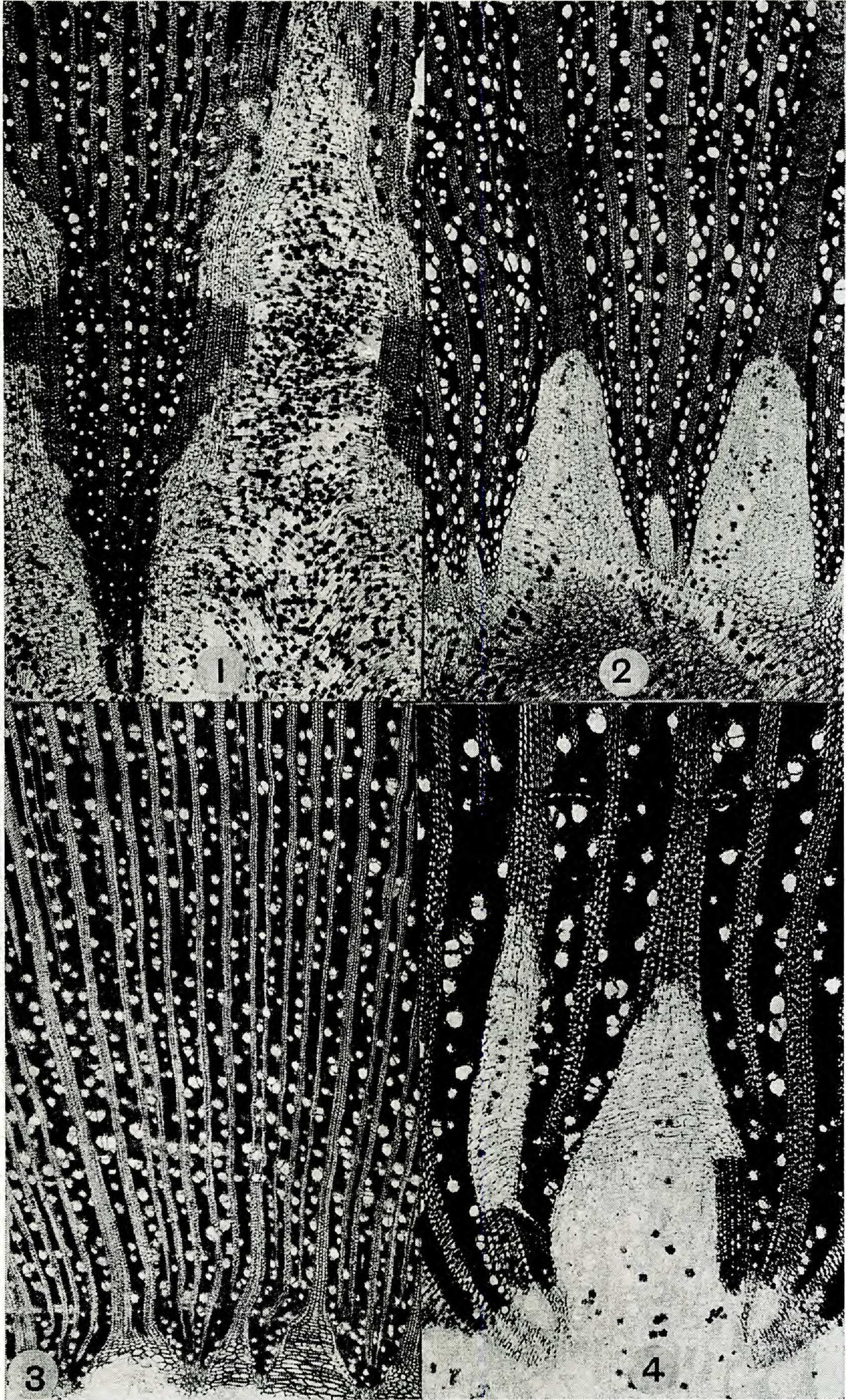
FIGS. 9, 10. Transverse sections of secondary xylem,  $\times 88$ . 9, *P. autumnalis* [Moore 8210] wood from stem 7 cm. in diameter. 10, *The same*, wood from stem 18 cm. in diameter.

## PLATE IV

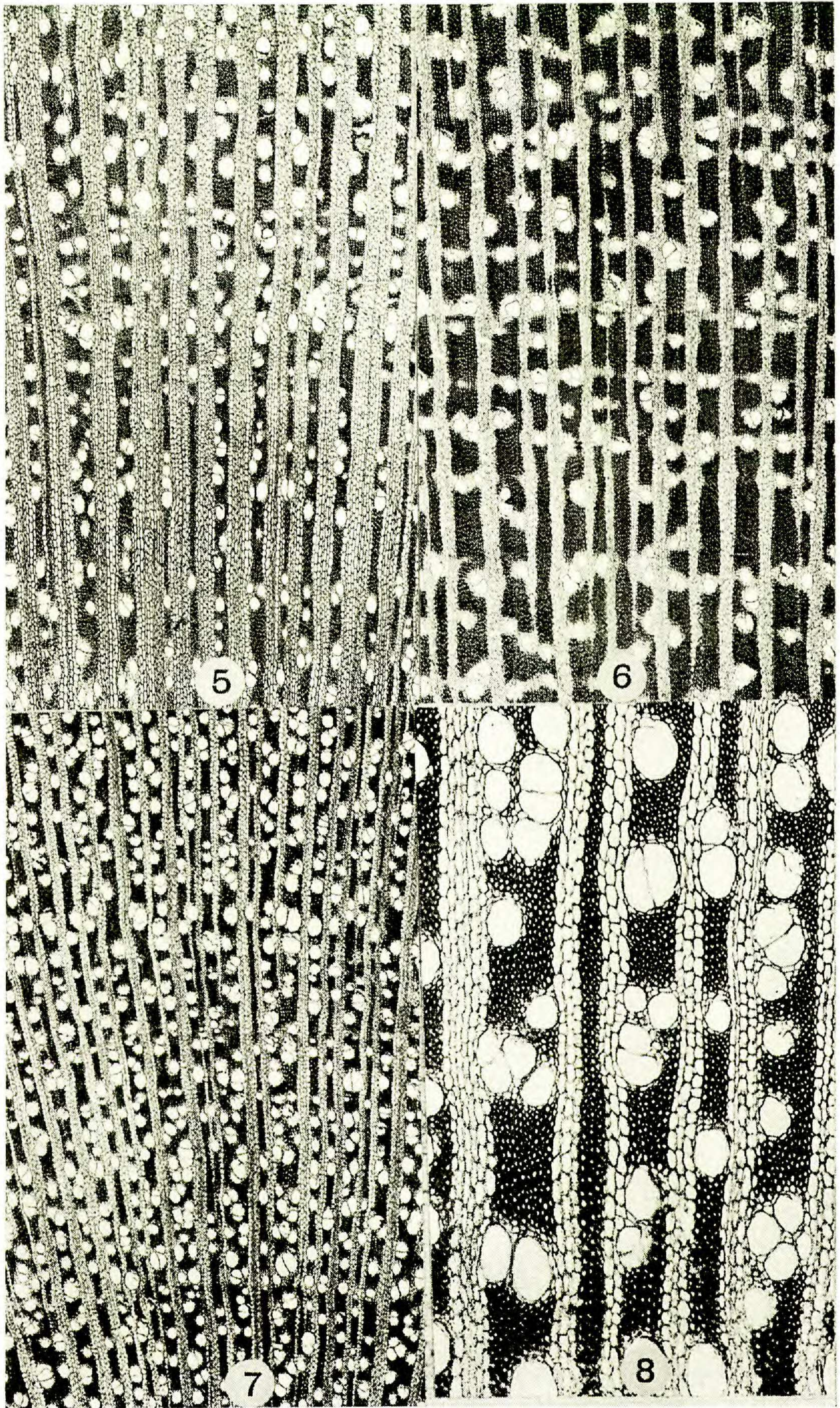
FIGS. 11, 12. Tangential longitudinal and transverse sections of secondary xylem. 11, *Pereskia nicoyana* [Rodríguez 662] tangential section of first-formed secondary xylem showing variation in multiseriate rays,  $\times 43$ . 12, *Pereskia conzattii* [Boke B-9] transverse section of outermost xylem of a very large stem,  $\times 34$ .

## PLATE V

FIGS. 13-16. Tangential longitudinal sections of secondary xylem. 13, *P. conzattii* [Boke B-9] showing form of multiseriate rays in outer xylem of a very large stem,  $\times 43$ . 14, *Pereskia nicoyana* [Rodríguez 662] showing form of rays in innermost secondary xylem,  $\times 11$ . 15, *Pereskia conzattii* [King & Diboll] form of rays in a stem 5 cm. in diameter,  $\times 43$ . 16, *Pereskia conzattii* [Sharp & Hernández] form of rays in a stem 7 cm. in diameter,  $\times 43$ .

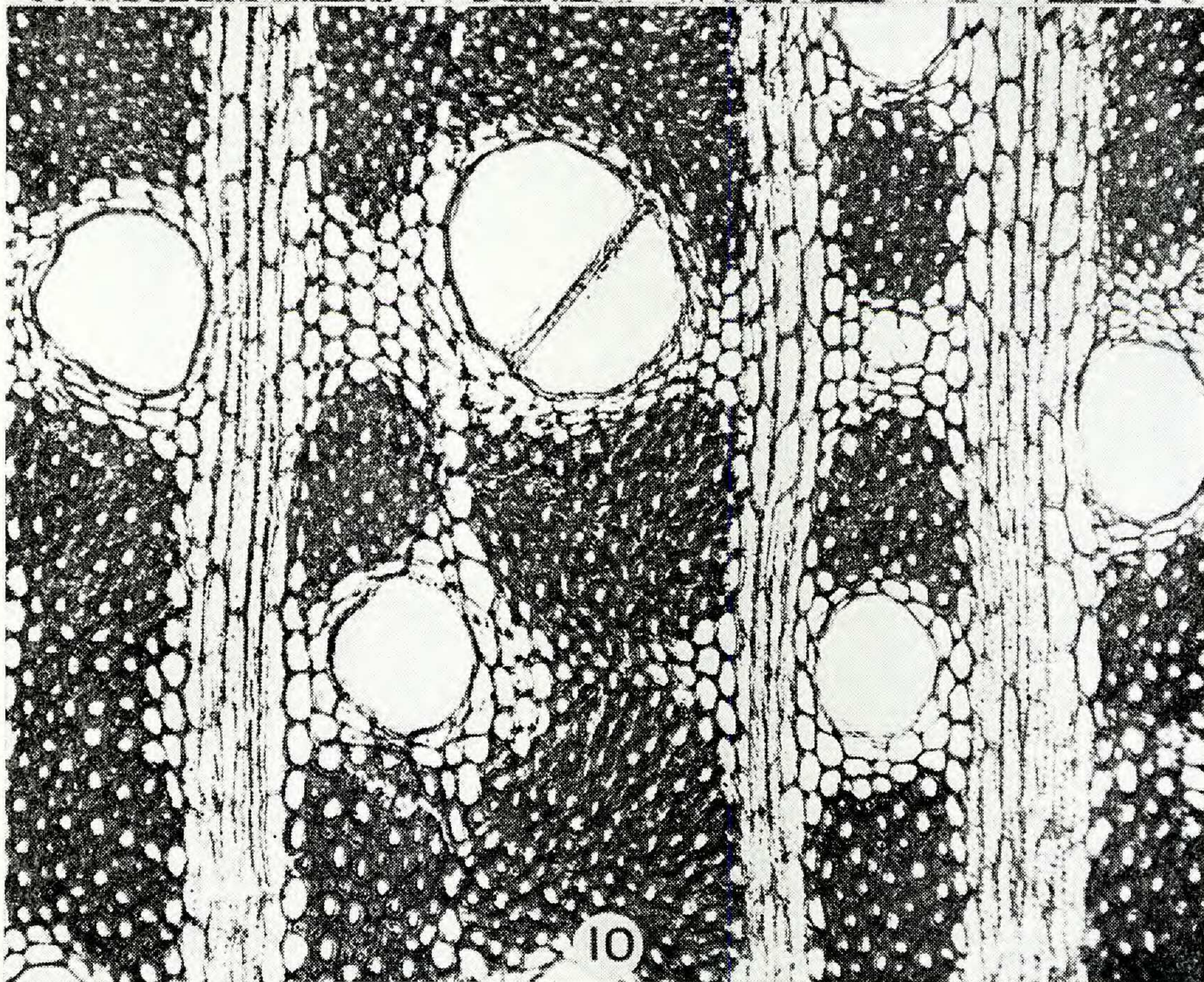
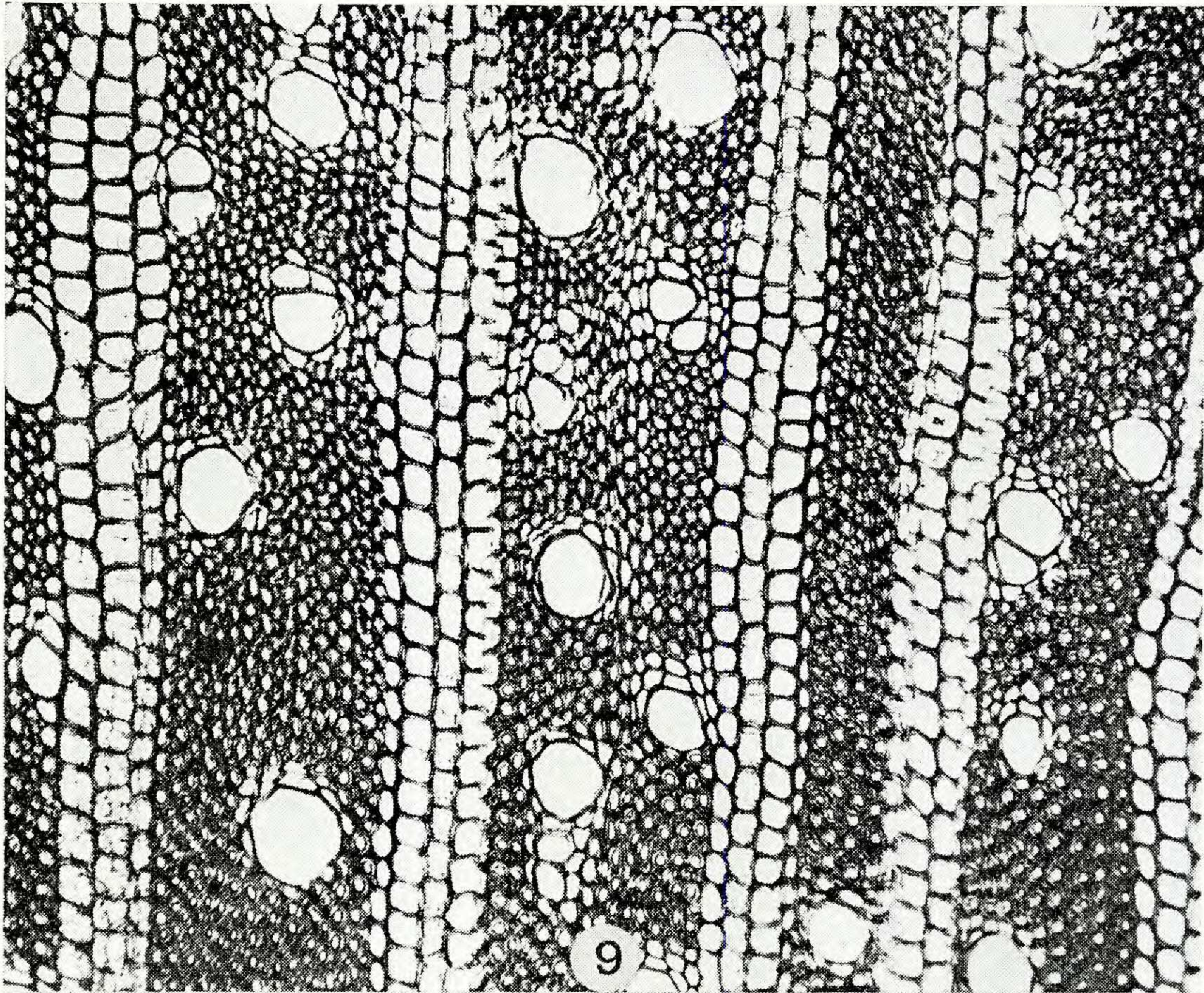


BAILEY, LEAF-BEARING CACTACEAE, VIII

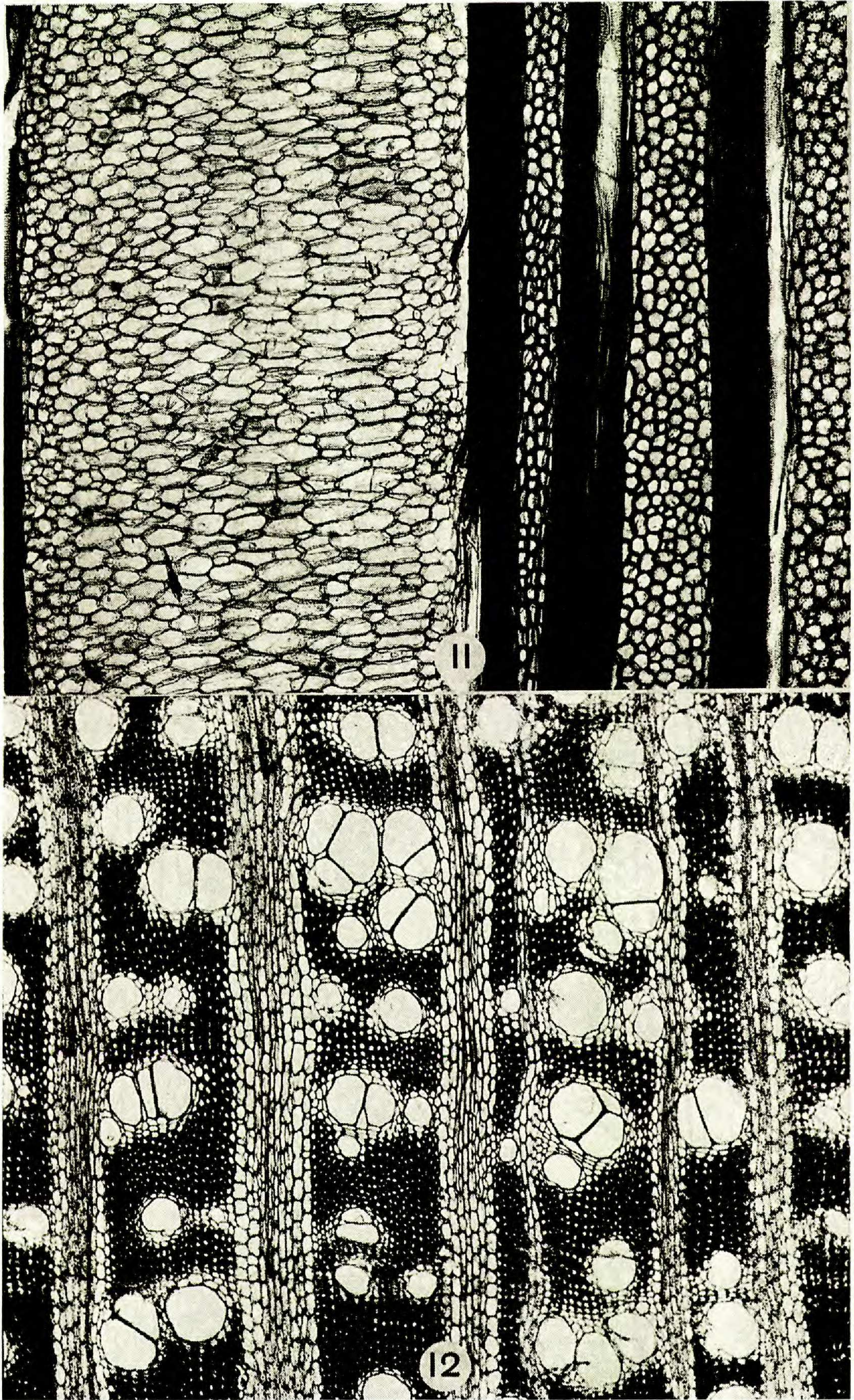


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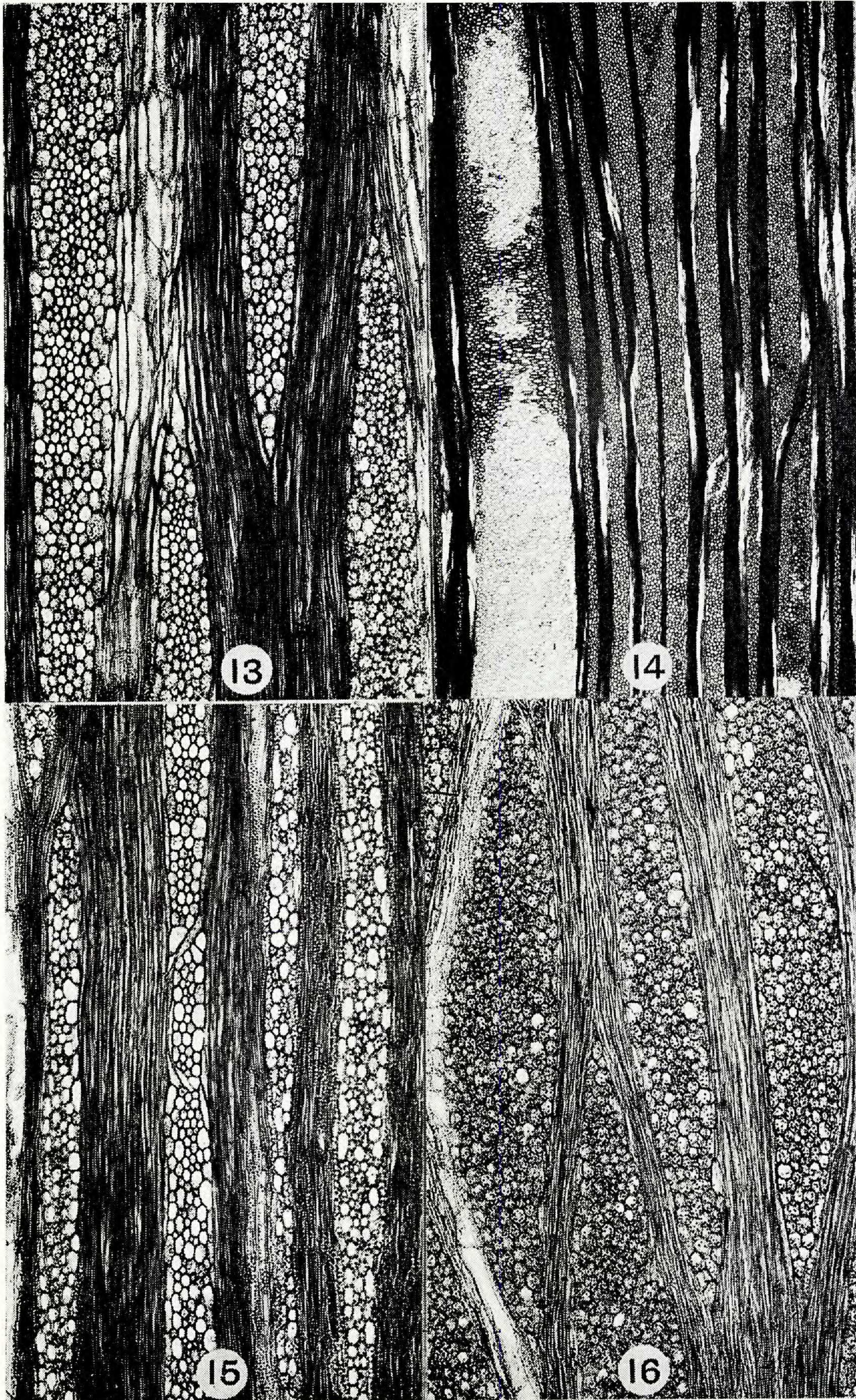




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